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REVISION OF THE PALAEOZOIC ORDER PAOLIIDA (INSECTA)

A. P. Rasnitsyn^{1,2)}, D. S. Aristov^{1,*}

1) *Borissak Paleontological Institute of the Russian Academy of Sciences, Profsoyuznaya str. 123, Moscow 117997, Russia. *Corresponding author, E-mail: danil_aristov@mail.ru*

2) *Natural History Museum, London, UK. E-mail: alex.rasnitsyn@gmail.com*

The order Paoliida (Insecta) is revised. A single family, Paoliidae from the Carboniferous of the United States and Europe, is included in this order. The order Paoliida is assigned to the infraclass Gryllones as the only order of the superorder Paoliidea Handlirsch, 1906, **stat. n.** The family Katerinkidae is synonymised under Paoliidae. The families Blatinopseidae **stat. resurr.**, Ideliidae, and Herbstiidae **stat. resurr.** are excluded from Paoliidae and placed in the orders Blatinopseida, Eoblattida and Cnemidolestida respectively. The family Paoliidae consists of 11 genera from the Carboniferous of North America and Europe.

KEY WORDS: Insecta, Gryllones, Paoliida, taxonomy, synonymy, new taxa, Carboniferous.

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Проведена ревизия отряда Paoliida (Insecta). В отряд включено только типовое семейство Paoliidae из карбона США и Европы. Paoliida отнесены к инфраклассу Gryllones как единственный отряд надотряда Paoliidea Handlirsch,

1906, **stat. n.** Семейство Katerinkeidae сведено в синонимы к Paoliidae. Семейства Blatinopseidae **stat. resurr.**, Ideliidae и Herbstialidae **stat. resurr.** исключены из паолиид и помещены, соответственно, в отряды Blatinopseida, Eoblattida и Cnemidolestida. В состав семейства Paoliidae входят 11 родов из карбона Северной Америки и Европы.

**Корреспондирующий автор, Палеонтологический институт им. А.А. Борисяка РАН, ул. Профсоюзная 123, Москва 117997, Россия.*

INTRODUCTION

The order Paoliida (Protoptera) occupies a special position in the system and phylogeny of Pterygota. It is the most ancient order of winged insects (the only order limited in its distribution to the Bashkirian and part of the Moscovian ages of the Carboniferous (Namurian B to Westphalian C-D of the European scale) and the most primitive group considered ancestral (or stem group) to other pterygotes (Sharov, 1966; Rasnitsyn, 1980; Rasnitsyn & Quicke, 2002) or exclusively to Neoptera (Grimaldi & Engel, 2005). Only Prokop *et al.* (2013), having radically reconsidered the composition of Protoptera, directly link this group to Dictyoptera. Protopterans were associated with ancient gymnosperms and fed on the contents of gymnosperm sporangia (Sharov, 1966; Rasnitsyn, 1980; Rasnitsyn & Quicke, 2002). Little is known about the morphology of protopterans apart from their wing venation and almost nothing is known about their ontogeny except for the single record of an isolated nymphal wing with venation very similar to that of the adult hind wing (Prokop *et al.*, 2012: fig 4A), pointing to very smooth metamorphosis, similar to that described for some palaeodyctiopterans (Sinitchenkova, 1979; Rasnitsyn & Quicke, 2002: fig. 71).

The purpose of this study is to re-examine the composition and structure of the order Paoliida in the light of the above-mentioned publication by Prokop *et al.* (2013), with whose conclusions we cannot agree. The analysis includes, in addition to doubtless paoliids, also Palaeozoic fossils assigned or considered close to Paoliidae by Prokop *et al.* (2013) or in some other publications and other species that can be considered close to Paoliidae in our opinion.

TAXONOMY

CLASS INSECTA LINNAEUS, 1758

INFRAClass GRYLLONES LAICHARTING, 1781

Superorder Paoliidea Handlirsch, 1906, **stat. n.**

DIAGNOSIS. Large insects with compact body, very long antennae, and elongate triangular wings folded roof-like. Folded wings overlapping only in anal areas, not parallel in imprints. Pronotum without paranota; legs long, clinging.

Forewing elongate, narrowing towards apex; all veins except *CuP* convex; *SC*, distal branches of *RS*, *M* and *CuA* situated on concave areas of membrane. Precostal area absent; costal area at base of *RS* wider than subcostal area. *SC* joining *R* (in some representatives of *Zdenekia* ending in bifurcation on *C* and *R*) in distal quarter of wing. *R* without posterior branches (except in *Sustaia*); *RS* beginning in basal third of wing (near wing middle in *Olinka*), usually with anterior branches in interrarial area. *M* starting branching near wing middle distal to base of *RS*; *M*₅ joining *CuA* proximal to its division into branches (in *Darekia* *M* and *CuA* fused over short distance). *CuA* weakly S-shaped, not divided into *CuA*₁ and *CuA*₂, sometimes with anterior branches in medial area and always with posterior branches in intercubital area. *CuA* pectinate posteriad, with anterior branch dichotomising, approaching hind angle of wing at angle of about 45°. Intercubital area dilated basally; *CuP* simple (in *Holasicia* with short fork).

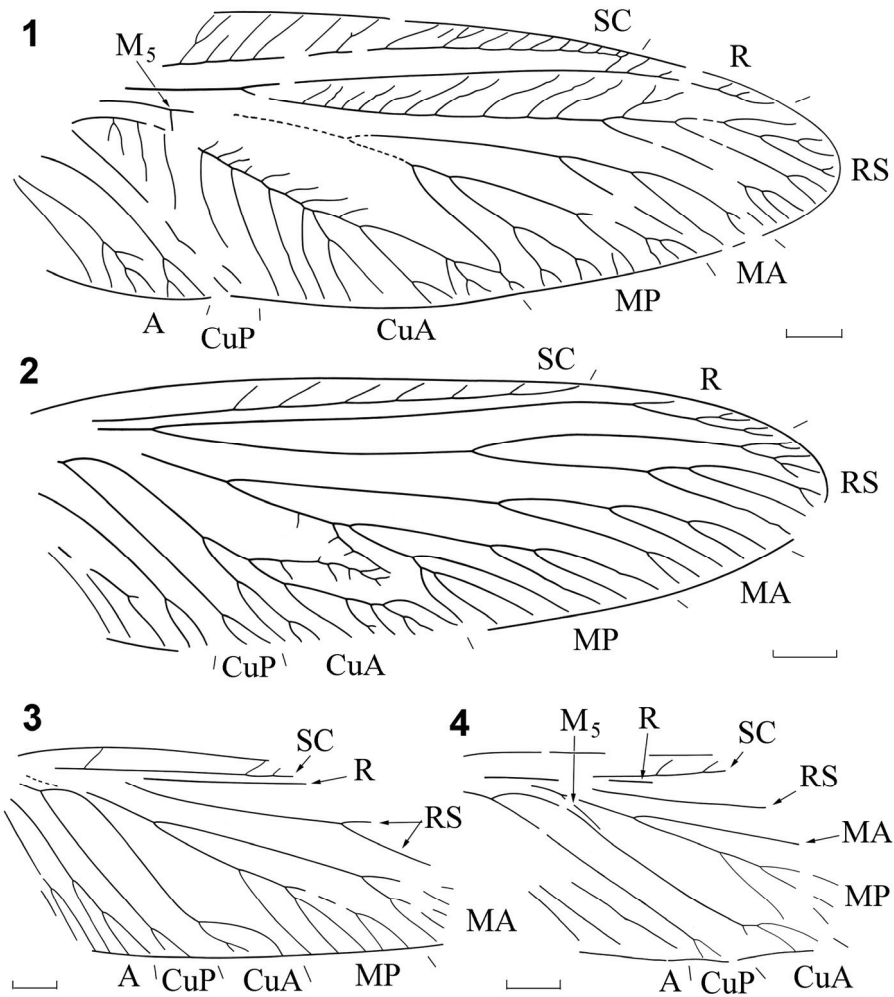
Hind wing more regularly and more broadly triangular than forewing; all veins weakly concave except convex *R* (and sometimes *RS*). *SC* ending on *C* (in *Paolia*), on *R* or in bifurcation (*Zdenekia*). *RS* beginning in basal quarter of wing, sometimes with blind branches in interrarial area. *M* branching in basal third of wing (in some representatives of *Zdenekia* closer to wing middle), posterior branch often blind or fused with *CuA*. *M*₅, if preserved, joining *CuA* or free, blindly ending in medial area. *CuA* smoothly S-shaped, starting branching distal to middle, sometimes with blind anterior branches (*Paolia*) or with blind anterior and blind posterior branches (*Zdenekia*, *Katerinka*). *CuP* with one or two short forks. Anal area not enlarged, not tucking down at rest. Crossveins forming archdictyon; veins with numerous terminal bifurcations.

COMPARISON. The superorder Paoliidea is distinguished from all other superorders of Gryllones mainly by the low roof-like folding of the wings, which are primarily homonomous (the hind wing is wider than the forewing but has no anal area tucked under the folded wing). In the other Gryllones, the wings are folded flatly or closely fitting the body and the hind wing has a large anal area tucking down at rest (in embiopterans, termites, and some stoneflies the wings have become secondarily homonomous). Representatives of the order Paoliida *sensu* Rasnitsyn (2002) are especially similar in body proportions, type of wing folding, and general venation pattern of the wings to primitive eoblattids of the family Cacurgidae, especially the Carboniferous genus *Kochopteron* Brauckmann, 1984 (Aristov, 2015). The only difference of cacurids from paoliids in characters of the body is the presence of paranota on the pronotum. In forewing venation, cacurids are distinguished by *SC* ending on *C* (without bifurcating), absence of anterior branches of *RS* and *CuA* in the interrarial and medial areas (perhaps except in *Kochopteron*) and *CuA* not pectinate posteriad. The main distinguishing feature of cacurids is the dilated (and probably tucking down in folded wings) anal area of the hind wing (known only in the type genus *Cacurgus*: Béthoux, 2006), which has a structure typical of Gryllones.

In adaptations to phytophily (elongate antennae and legs, developed arolium and moderately roof-like folding of the wings), paoliids are similar to mantises, especially the Permian Permophasmataidae (Aristov & Rasnitsyn, 2015) and differ from most

of them not only in venation, but also in proportions of the body. Like permophasmatids, paoliids have very long legs and short bodies, while other mantises have the length of the legs and body correlated.

COMPOSITION. The order Paoliida only.



Figs 1–4. Family Paoliidae. 1 – *Zdenekia grandis* Kukalova, 1958, holotype MMO No. B1006, forewing; 2 – *Paolia vetusta* Smith, 1871; 3 – *Paolia* cf. *vetusta* Smith, 1871, specimen NNMN No. B1002 (original drawing based on photograph Prokop *et al.*, 2013); 4 – *Paolia* sp., spec. MGPV, Aivon 6 (original drawing based on photograph Prokop *et al.*, 2014). Scale bar in fig 1- 10 mm, in figs 2-11 - 5 mm.

NOTES. Paoliids were treated as an order of Pterygota not assigned to any infraclass (Rasnitsyn, 2002) or as representatives of the infraclass Neoptera Martynov, 1923 (Prokop *et al.*, 2012). In our opinion, the similarity of paoliids to primitive eoblattids (see above) and the smooth transition between the two groups makes it possible to assign the order Paoliida to the infraclass Gryllones as the most primitive order, ancestral to the other Gryllones. At the same time, the low roof-like folding of the wings, which is atypical of the other Gryllones (except the primitive cacurgids), and the anal lobe of the hind wing not tucking down, in contrast to the majority of Gryllones, suggest assigning paoliids to a separate superorder Paoliidea of Gryllones. The latter character is unknown in cacurids, and the position of wings at rest in Carboniferous fossils is rarely reliably known; therefore, in practice paoliids are distinguished from the lower Gryllones in the absence of paranota in combination with *SC* that joins *R* rather than *C* (see above).

The question of the relationship of paoliids to the infraclass Scarabaeones (cohorts Cimiciformes and Scarabaeiformes) is no less complicated. We see here no such smooth transition as between Paoliidae and Cacurgidae, but we know no such apomorphies of paoliids that would refute treating them as ancestral to Scarabaeones (Rasnitsyn, 2002). There are some fossils that more or less bridge the gap between the two taxa, above all *Stygne* Handlirsch, 1906 and *Evenka* Rasnitsyn, 1983, which have the anal lobe in the forewing rather small, not tucking down, and such archaic characters as the anterior blind branches of *RS* (*Stygne*) or free *M*₅ (*Evenka*), but at the same time also very large *RS*, typical of early Scarabaeones, but not of archaic Gryllones (Rasnitsyn & Quicke, 2002). Therefore, we consider the two above-mentioned genera as in Rasnitsyn & Quicke (2002), i.e. as basal Scarabaeones (presumably basal Cimiciformes), without specifying their taxonomic position in more detail.

Therefore, theoretically the differences of Scarabaeones from Paoliida and Gryllones in general remain clear and deep (Scarabaeona having such synapomorphy as the invagination of the sternite of the pterothorax, originally partial invagination, with the formation of the discrimen and corresponding internal ridge that bears a furca: see Rasnitsyn & Quicke, 2002). However, in practice distinguishing between them is even more difficult than distinguishing between paoliids and cacurids, because the fine morphology of the pterothorax is poorly preserved in Carboniferous insect fossils.

Order Paoliida Handlirsch, 1906

Paoliida: Rodedndorf, 1977: 19; Rasnitsyn, 1980: 30; 2002: 83; Prokop & Nel, 2007: 79; Prokop *et al.*, 2012: 163; 2013: 2; 2014: 159.

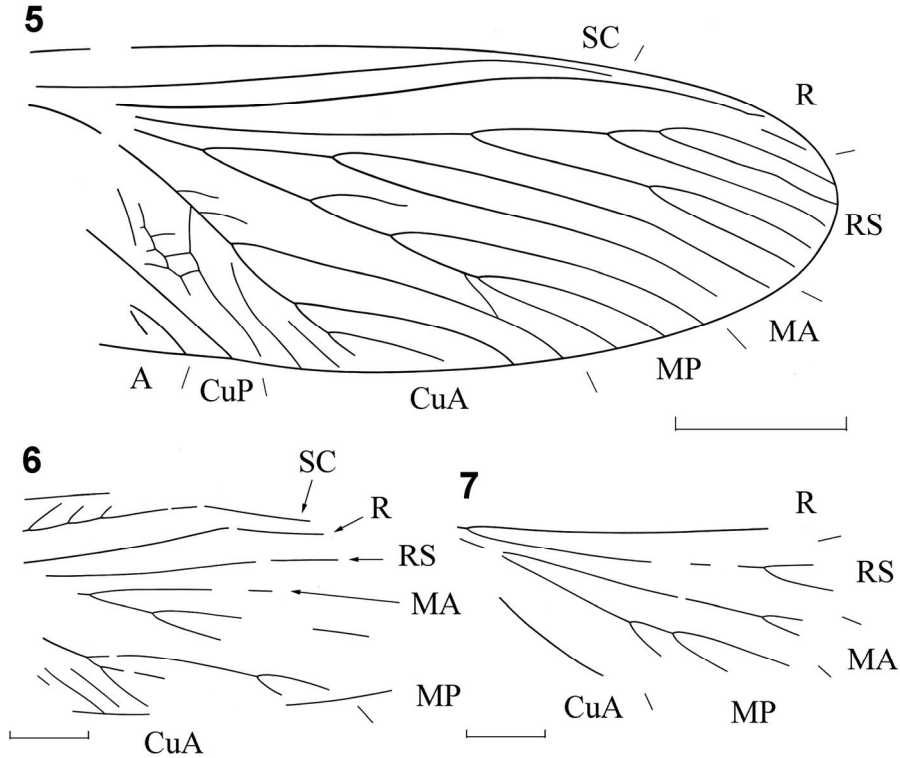
Protoptera: Sharov, 1968: 8; Gorochoy, 2004: 7.

DIAGNOSIS. Same as for superorder.

COMPOSITION. The family Paoliidae only.

NOTES. Recently the family Blattinopseidae (order Blattinopseida: Rasnitsyn, 2002), and Herbstiidae (incertae ordinis: Aristov, 2014) were synonymised under

Paoliidae and some genera of the family Ideliidae (order Eoblattida: Aristov, 2015) were transferred to Paoliidae (Prokop *et al.*, 2013). In addition the type genus of family Protoblattinidae was transferred to Paoliidae, but Protoblattinidae was not synonymised under Paoliidae (Prokop *et al.*, 2013).



Figs 5–7. Paoliida and Eoblattida incertae sedis. 5 – *Pseudofouquea cambrensis* (Allen, 1901), holotype MPG 7272 (original drawing based on photograph Bolton, 1921); 6, 7 – “*Pseudofouquea*” sp., spec. LL 11171 (original drawing based on photograph Anderson *et al.*, 1997): 6 – forewing, 7 – hind wing.

We don’t agree with these suggestions. It has been shown that the pterothorax of Blattinopseidae has a complete midventral furrow (discrimen) typical of the infraclass Scarabaeones; other peculiar features of Blattinopseidae are also in agreement with this fact (the wings folded in a high roof-like manner; the hind wing with a dilated anal lobe tucking down behind 2A; and cutting ovipositor with free sheaths (Rasnitsyn, 1980; Rasnitsyn & Quicke, 2002). The family Ideliidae (Eoblattida: Aristov, 2015) differs from Paoliidae in both the body and wings. It is characterised by the pronotum with paranota and by the non-clinging legs of moderate length (the mesotibiae and metatibiae are directed posteriad: Rasnitsyn & Krasilov, 1996; Aristov,

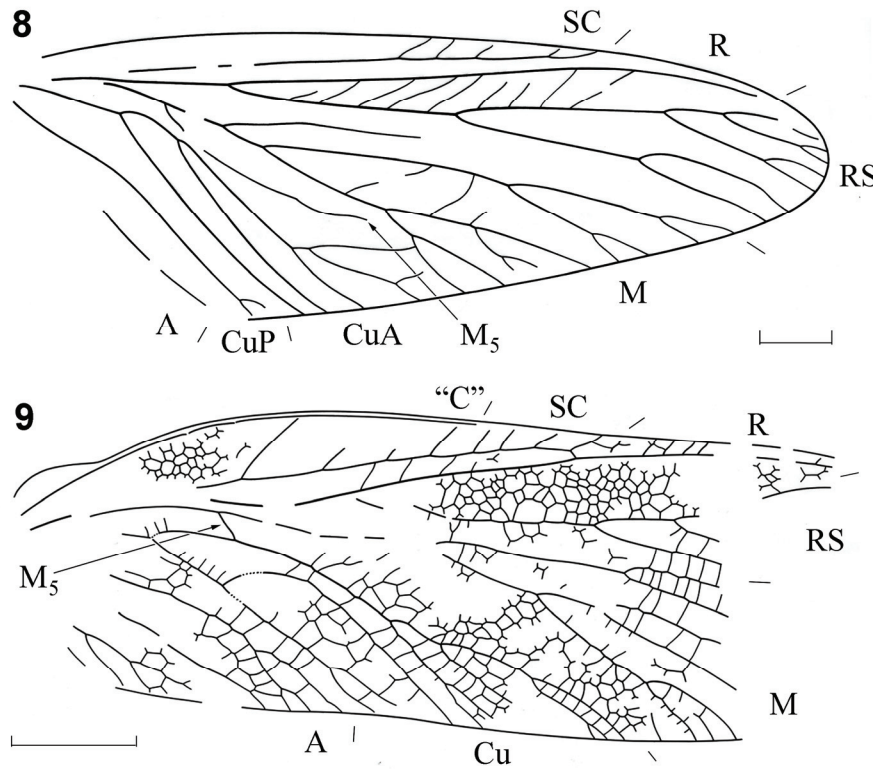
2002). The family Ideliidae, including the genera assigned by Prokop *et al.* (2013) to Paoliidae, are characterised by flatly folded broadly overlapping wings and the anal lobe of the hind wing wide, tucking down at rest, as in advanced Gryllones (dilated and posteriorly tucked *1A*). In the forewing, *SC* ends on *C*, *RS* has no blind branches in the interrarial space, and *M* divides in the basal quarter of the wing (Storozhenko, 1998). The anal area of the hind wing is large, tucking down. In our opinion, this excludes the possibility that they belong to Paoliidae. When ideliids were synonymised, some genera of this family (*Rachimentomon* Zalesky, 1939, *Kolvidelia* Zalesky, 1956, *Ideliopsina* Storozhenko, 1997, *Anaidelia* Storozhenko, 1997, *Madygenidelia* Storozhenko, 1997 and *Pseudoshurabia* Storozhenko, 1997) were excluded from Paoliidae based on the narrower intercubital area, reduced wing venation (*Kolvidelia*; in fact we can see no reduction there) or insufficient preservation quality (*Rachimentomon*). The genera *Ideliopsina*, *Anaidelia*, *Madygenidelia*, and *Pseudoshurabia* were described from Madygen, a locality that typically yields imprints with proportions distorted because of the deformed surrounding rock. In our opinion, the width of the intercubital area, especially if the fossil is of this preservation type, is insufficient for rejecting relatedness to the other Ideliidae. All the above-listed genera comply with the diagnosis of Ideliidae and should be treated within this family.

The hind wing of Protoblattinidae is unknown, but the presence of paranota, forewing not narrowing towards the apex and lacking blind branches of *RS* and *CuA*, *SC* ending on *C*, rather proximally branching *M* and rather distally branching *CuA* make it impossible to assign this family to Paoliida.

Herbstiala herbsti (Herbstialidae: Schmidt, 1953) from Sophia Jacoba (Westphalian A of Germany) was assigned to Paoliida, and the family Herbstialidae was synonymised under Paoliidae (Prokop *et al.*, 2013). Re-examination of a photograph of *H. herbsti* has shown that this insect has a precostal area separated by a very long “C”, no blind branches of *RS* in the intercubital area, unique *Cu* that has three main branches, the second of them of absolutely unclear homology, and clavus (Fig. 9). *Herbstiala* is similar in some characters (the presence of the precostal area, *SC* ending in bifurcation on *R* and *SC*, and clavus) to some families of Cnemidolestida. The precostal area and bifurcated *SC* are typical of Juraperlidae, *SC* ending on *C* and *R* is found in most representatives of Cnemidolestida, clavus is known in Cnemidolestidae, Cimenophlebiidae and others. However, the structure of the cubitus makes it impossible to assign *Herbstiala* either to Cnemidolestida or to any other known order of Gryllones.

The genus *Katerinka* Prokop *et al.*, 2007, judging by the concave and rather distally branching *CuA* and by the sharply narrowing wing, was described from an incomplete hind wing with the anal area typical of Paoliidae. This genus was assigned to a separate family Katerinkidae, distinguished from Paoliidae by the short *SC* and wide costal area (Prokop & Nel, 2007). Judging by the photograph (Prokop & Nel, 2007: fig. 6), *SC* runs to the distal one-third of the wing, where it approaches *C*. Otherwise, *Katerinka* is characterised by posterior branches of *R*, which are atypical of Paoliidae (known only in the forewing of *Sustaia*) and by *RS*

beginning rather distally, distal to the first bifurcation of *M*. In the other paoliids, the base of *RS* is basal to the first bifurcation of *M*. In our opinion, these characters, especially in the hind wing, are insufficient for preserving for the genus *Katerinka* a separate family, which is therefore synonymised here under Paoliidae. The suggestion that *Katerinka* is closely related to Camptoneuritidae (Prokop *et al.*, 2013) is unjustified, because Camptoneuritidae (as well as all Reculida *sensu* Aristov, 2015) are characterised by the absence of posterior branches of *R* or *CuA* and presence of the tucking down anal area.



Figs. 8, 9. Paoliida and Gryllones incertae sedis. 8 – *Paoliola gurleyi* (Scudder, 1885), holotype FM No. PE 6393, hind wing (original drawing based on photograph Prokop *et al.*, 2013); 9 – *Herbsitala herbsti* Schmidt, 1953, holotype GD NRW No. Kar 46, forewing (original drawing based on photograph by J. Prokop).

Pseudofouquea cambrensis Handlirsch, 1906, described from the hind wing (Fig. 5), is characterised by *SC* joining *R* and by the anal area rather small. This species is distinguished from the other Paoliidae by a unique combination of anterior and posterior branches of *CuA* and by the simple *CuP*. In addition, *Pseudofouquea*

is characterised by one posterior branch of *R*. *Paoliola gurleyi* (Scudder, 1885), also known from the hind wing, differs from Paoliidae in *SC* ending on *C* and in *CuA* branching twice and rather proximally (Fig. 8). At the same time, the presence of free branches on *RS*, free *M*₅, and rather small anal area indicate the archaic level of this species, similar to the level of Paoliidae. Because of these differences, we assign *P. gurleyi* and *P. cambrensis* to Paoliida incertae familiae, since it would be untimely to recognise separate families for these species.

Family Paoliidae Handlirsch, 1906

Paoliidae Handlirsch, 1906: 682; Kukalová, 1958: 935; Sharov, 1968: 8; Rasnitsyn, 1980: 30; Brauckmann, 1991: 184; Carpenter, 1992: 101; Rasnitsyn, 2002: 83; Gorochoy, 2004: 10; Prokop & Nel, 2007: 79; Prokop *et al.*, 2012: 163; Prokop *et al.*, 2013: 3; Prokop *et al.*, 2014: 159.

Katerinkidae Prokop & Nel, 2007: 82; Prokop *et al.*, 2013: 17; **syn. n.**

Type genus: *Paolia* Smith, 1871.

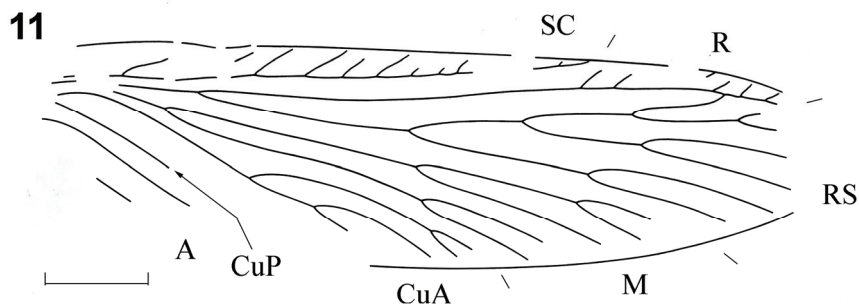
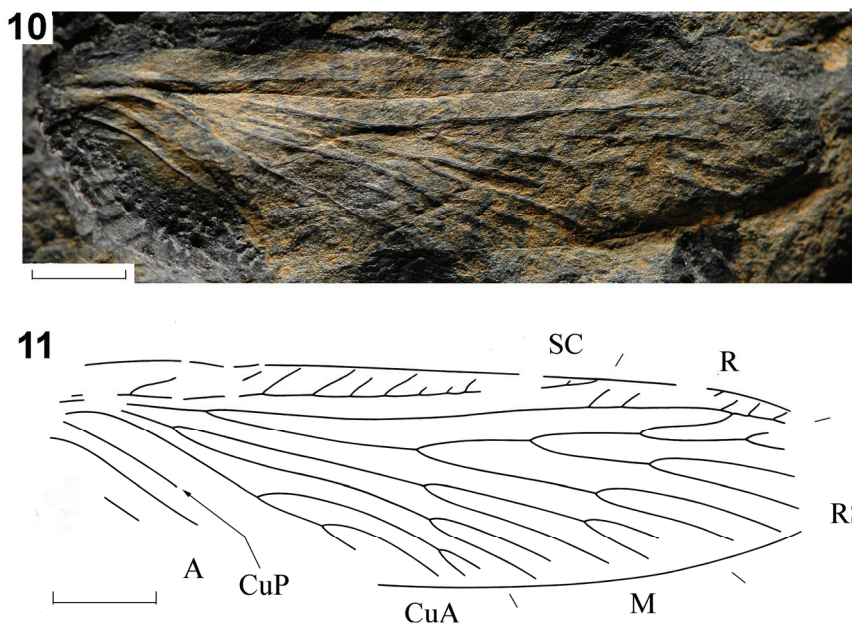
DIAGNOSIS. Same as for superorder.

DESCRIPTION. Head rather small, hypognathous, with rather small eyes, very long antennae (longer than forewing) with elongate antennomeres, and long maxillary palpi. Pronotum is rather small, trapezoid, comparable in size to head. Mesonotum rather small, wider than long. Tibiae directed anteriad; legs very long; forelegs and midlegs similar in length. Procoxae closely set; tibia slightly longer than femur; tarsus somewhat shorter than femur. Tarsus five-segmented; tarsomere 1 longer than any other tarsomere; tarsomeres 3 and 4 shorter than any other tarsomere. Apices of tarsomeres 2–4 with pulvilli, apex of tarsomere 5 with arolium and claws. Forewing with anterior margin convex; costal area wider than subcostal area; *SC* ending in distal quarter of wing. *R* without posterior branches (except in *Sustai* Kukalová, 1958). *RS* beginning in basal one-third of wing (near middle in *Olinka* Kukalová, 1958), dividing in distal one-third of wing less abundantly than *CuA*. *M* not divided into *MA* and *MP*, with rather few branches. Stems *RS* and *M* sometimes strongly concave. *CuP* usually concave, sometimes situated inside fold separating clavus (in *Darekia* Prokop *et al.*, 2012).

COMPOSITION. Eleven genera from Upper Carboniferous of North America and Europe: *Paolia* Smith, 1871 from French Lick (= Braxton Quarry, United States; Morrowan Stage, corresponding to Namurian C in Europe), from Hendrik Mine (Westphalian A of the Netherlands) and from Avion, Terril No. 7 (Westphalian C-D of France); *Zdenekia* Kukalová, 1958 from Horní Suchá (Westphalian A of the Czech Republic), Sosnowiec-Klimontów (Westphalian A of Poland), and Charbonnages de Ressaix (Westphalian A of Belgium); *Sustaia* Kukalová, 1958; *Olinka* Kukalová, 1958 from Horní Suchá; *Holasicia* Kukalová, 1958 from Horní Suchá and Hagen Vorhalle (Namurian B of Germany), *Kemperala* Brauckmann, 1984 from Hagen Vorhalle; *Mertovia* Prokop *et al.*, 2007 from Hlubiná Pit (Westphali-

an A of the Czech Republic), *Katerinka* Prokop et Nel, 2007 from Doubrava Mine (Namurian–Westphalian of the Czech Republic); and possibly *Darekia* Prokop *et al.*, 2012 from Sosnowiec-Klimontów.

NOTES. We exclude from the family Paoliidae several species described in this family or formerly assigned to it. For instance, *Paolia superba* Scudder 1885 from the Naperville locality (Francis Creek Shale Member [Carbondale Formation], Westphalian D) was assigned to a separate genus, *Parapaolia* (Protorthoptera: Palaeocixiidae; Carpenter, 1951), which was subsequently treated as Palaeoptera incertae ordinis (Carpenter, 1992). *Parapaolia* is characterised by the forewing with SC ending on C and oligomerised CuA without posterior branches and hind wing typical of Gryllones. This genus is probably closely related to Cymenophlebiidae of the order Cnemidolestida (Aristov, 2014).



Figs 10, 11. *Paolia lacoana* Scudder 1885, holotype NMNH 038100 (original drawing based on photograph by A.P. Rasnitsyn).

The genus *Silesiapteron* was described in Paoliidae from the Westphalian locality Sosnowiec-Klimontów in Poland (Prokop *et al.*, 2013). This genus is characterised by several posterior branches of *R* and by *CuA* pectinate posteriad, with one blind posterior branch and the distal branch pectinate anteriad. As noted above, posterior branches of *R* are atypical of paoliids. This structure of *CuA* is very characteristic of the eoblattid family Ideliidae (see above), and several posterior branches of *R* in com-

bination with a single posterior branch of *CuA* are characteristic of some Bardapteridae of the same order (Aristov, 2015). *Silesiapteron* probably represents a separate family of Eoblattida, closely related to Ideliidae and Bardapteridae and different from them mainly in *M* branching distal to the middle of the wing and in the presence of the clavus. Similar structure of *CuA* in the forewing is characteristic of *Pseudofouquea* sp. from the Carboniferous of the United Kingdom (Andersen *et al.*, 1997). *CuA* of the hind wing of this specimen (Figs. 6, 7) is simple or dividing very distally, which makes it impossible to assign it to *Pseudofouquea*. As for the forewing venation, it is similar to that of *Silesiapteron* and differs from it in the more basal bifurcation of *M*. Because this specimen is incompletely preserved, we assign it to Eoblattida incertae sedis.

Kochopteron hoffmannorum Brauckmann, 1984 from the Namurian locality Hagen-Vorhalle (Germany) was described in the family Cacurgidae (Brauckmann, 1984) and subsequently assigned to Paoliidae (Prokop *et al.*, 2013). *Kochopteron* differs from paoliids in the presence of paranota of the pronotum and in *SC* of the forewing without terminal bifurcation ending on *C*. Cacurgidae, including *Kochopteron*, have been assigned to primitive Eoblattida (Aristov, 2015).

Protoblattinopsis stubblefieldi Laurentiaux, 1953 from South Staffordshire (Westphalian B of the United-Kingdom) was also assigned to Paoliidae (Prokop *et al.*, 2013). This species is characterised by the hypertrophied media that starts branching in the basal quarter of the wing and forms an anastomosis with the posterior branch of *RS*, by reduced *Cu* without clear anterior and posterior oblique branches of *CuA*, and rudimentary anal area of the forewing, characters absolutely atypical of paoliids (Béthoux *et al.*, 2009). The size of the preserved fragment makes it impossible to reconstruct the shape of the wing (whether it was elongate triangular, which is characteristic of paoliids). We treat this species as Gryllones incertae familiae.

Paolia lacoana Scudder 1885 (Figs. 10, 11) was described from the locality Campbells Ledge (= Pittston: United States, Pennsylvania; Upper Carboniferous, Atokan Stage [Westphalian C], Pottsville Formation). The genus *Pseudopaolia* was subsequently described for this species (Handlirsch, 1906). When the type was re-examined, *P. lacoana* was transferred from Palaeoptera of order uncertain (Carpenter, 1992) to Caloneurida, but simultaneously mistakenly designated in the figure caption as *Paoliola gourlei* Handlirsch (Rasnitsyn & Quicke, 2002: 108, fig. 115).

We agree with Carpenter (1992), who assigned the Permian *Paolekia perditae* Riek, 1976 from South Africa, originally placed in Paoliidae (Riek, 1976), to “Protorthoptera of family uncertain”.

Prokop *et al.* (2013) provided a checklist of Palaeozoic insects potentially attributable to Paoliida. In addition to those that were explicitly included in the family Paoliidae or order Paoliida and have been discussed above (Blattinipseidae), these include *Camptoneurites reticulatus* (Martynov, 1928) (Reculida: Camptoneuritidae; Aristov, 2015), *Demopterum gracile* Carpenter, 1950, currently also included in Camptoneuritidae (Aristov *et al.*, 2010), and *Stygne* (see above). The forewings of Camptoneuritidae, as well as Protoblattinidae, discussed above, are

characterised by *SC* ending on *C*, rather proximal (proximal to base of *RS*) branching of *M*, and distal branching of *CuA*. These characters make it impossible to assign *Camptoneuritidae* to *Paoliida*.

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